Photosynthetic response of *Pinus sylvestriformis* to elevated carbon dioxide and its influential factor analysis

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Abstract: The photosynthetic response of 12-year old *Pinus sylvestriformis* to elevated CO_2 and its influential factors were tested and analyzed in the forest region of Changbai Mountain in 1999. Trees grown at the natural condition were controlled at three levels of CO_2 concentration (350 $\mu L \cdot L^{-1}$, 500 $\mu L \cdot L^{-1}$ and 700 $\mu L \cdot L^{-1}$) by CO_2 rich settlement designed by us. Net photosynthetic rates (NPR), temperature, relative humidity, stomatal conductance, intercellular CO_2 concentration and photosynthetic active radiation (PAR) were measured at 6:00, 8:00, 10:00, 14:00, 16:00 and 18:00 hours a day. Experimental results showed that the NPR of *Pinus sylvestriformis* increased by 32.6% and 123.0% at 500 $\mu L \cdot L^{-1}$ and 700 $\mu L \cdot L^{-1}$ CO_2 concentration respectively, compared to ambient atmospheric CO_2 concentration (350 $\mu L \cdot L^{-1}$). The relations between NPR and influential factors, including temperature, relative humidity, intercellular CO_2 concentration and photosynthetic active radiation, were analyzed respectively by regression analysis at different CO_2 concentrations.

Keywords: Photosynthetic response; Influential factors analysis; *Pinus sylvestriformis;* Elevated carbon dioxide
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Introduction

Our world is changing in the way and at the speed that are describable, but we are unable to predict these changes with any degree of accuracy. Radioactive and chemical properties of the atmosphere, global climate, and global ecology are dynamic and measurable, but they also linked to each other in complex and poorly understood ways (Raval and Ramanathan 1989). While many of the physical and biological sub-processes are understood and modeled in detail, predictive capabilities are poor if we do not understand the linkages. There is no consensus as to either how or how much global climate might change as a consequence of alterations in atmospheric chemistry or whether changes in atmospheric chemistry or bode net good or net ill for mankind (Lindzen 1990). One cannot now predict reliably how simultaneous changes in both chemical or climate drivers will alter the biosphere by changing biomass accumulation, species diversity or ecosystem structure.

Evidence from many source shows that the concentration of atmospheric CO_2 is steadily rising, which strongly relates to the increase in global consumption of fossil fuels and also gets significant contributions from the clear cutting of forests. Most scientists agree that rising CO_2 levels will have substantially direct and indirect effects on the biosphere. CO_2, as a greenhouse gas, may influence the earth energy budget when it increases in the atmosphere. However, regardless the changes in global temperature and other climate variables, rising CO_2 can influence world ecosystems by direct effects on plant growth and development (Bazzaz 1990).

When other environmental resources and factors are preset in adequate level, CO_2 can enhance photosynthesis of C_3 plants over a wide range of concentrations. High CO_2 reduces competition from O_2 for Rubisco, increases its activation (Pearcy *et al.* 1993), and reduces photorespiration. In contrast, in plants with the C_4 metabolism the net photosynthetic rates rise steeply above ambient (Tolbert *et al.* 1983).

Early studies concentrated on the response of plants to elevated CO_2 levels of glasshouses and growth chambers. Current studies mostly make use of use plants grown under controlled CO_2 levels. All these studies showed that the photosynthetic rates increase with increase of CO_2 concentration. More and more reports showed that the photosynthetic response of plant to elevated CO_2 was different ob-

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viously due to the different species of plant especially to their stage of life. *Pinus sylvestriformis* grows on the northern slope of Changbai Mountain at altitudes of 800~1 000 m and has formed small pure forest beside Erdaobaihe. At the altitude of 1 600 m, this species mixed with *Pinus koraiensis* and *Picea jezoensis*. The growth rate of its seedlings is similar to *Larix olgensis* and more rapid than *Pinus koraiensis*. The quality of *P. sylvestriformis* wood is good, easy to be processed and hard to be eroded. The research on effects of elevated CO_2 on *P. sylvestriformis* is limited to its young growth stage (Wang *et al.* 1999; Han *et al.* 1999). Few studies on the effects of elevated CO_2 on mature *Pinus sylvestriformis* were reported. This paper studies the photosynthetic response of *Pinus sylvestriformis* to elevated CO_2.and its influential factors.

Materials and methods

Experimental objective is 12-year old *Pinus sylvestrifomis* grown under natural condition. CO_2 used in this experiment was produced by Jilin New Star Liquid Carbon Limited Corporation that purified from natural CO_2 gas, with a purity of 99.9%.

The experiment was conducted in the Opened Research Station of Changbai Mountain Forest Ecosystems (128°06' E, 42°24' N), Chinese Academy of Sciences, at altitude of 738.1 m, in September 1999. Atmospheric CO_2 concentration in this region is approximately 350 $\mu L \cdot L^{-1}$. Environmental CO_2 concentration was controlled at the levels of 350 $\mu L \cdot L^{-1}$ (contrast), 500 $\mu L \cdot L^{-1}$ and 700 $\mu L \cdot L^{-1}$. Firstly, we put CO_2 gas into a big plastic sack from CO_2 tank. Then CO_2 gas was pumped into spiral pipe (D = 2.5 cm) that circled the canopy and has holes (D = 2.5 mm) inside. CO_2 flow towards leaf via holes. We adjusted the pipe gas valves and hole number to control the concentration of CO_2.

On calm or breeze days, three parallel measurements were made with CI-301CO_2 gas analyzer, at 6:00, 8:00, 10:00,12:00, 14:00 and 18:00 hours. Light source was sunlight and open system was used in observation. The observed Indices include net photosynthetic rate, temperatures, relative humidity, stomatal conductance, intercellular CO_2 concentration and photosynthetic active radiation (PAR).

Data was proceeded with Excel software.

Results and analysis

Daily changes of NPRs of *P. sylvestriformis* at deferent CO_2 concentrations

The statistical data shows that the NPR of *Pinus sylvestriformis* increased averagely by 32.6% at 500 $\mu L \cdot L^{-1}$ CO_2 and by 123% at the concentration of 700 $\mu L \cdot L^{-1}$ CO_2, (Table 1). These results indicated that NPR of *Pinus sylvestriformis* increased with the elevation of environmental CO_2 concentration. The peak value of NPR at 350 and 500 $\mu L \cdot L^{-1}$ CO_2 occurred at 8:00 O'clock, while at concentration of 700 $\mu L \cdot L^{-1}$ CO_2 the highest NPR occurred at 10:00 (Fig. 1), which indicated that the elevated CO_2 promoted the CO_2 assimilation saturation point.

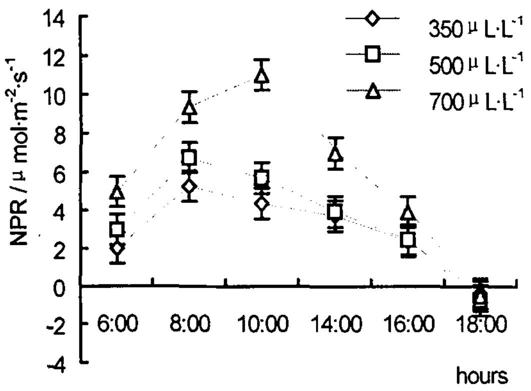

Fig.1. Daily changes of the NPR of *Pinus sylvestriformis* at different CO_2 concentrations

Influential factor analysis of NPR of *Pinus sylvestriformis* under elevated CO_2

Daily changes of temperature, relative humidity, intercellular CO_2 concentration and photosynthetic active radiation at different CO_2 concentrations were observed and shown in Table 2.

Table 1. NPR of *Pinus sylvestriformis* at CO_2 concentrations of 350 $\mu L \cdot L^{-1}$, 500 $\mu L \cdot L^{-1}$ and 700 $\mu L \cdot L^{-1}$

Time	350 $\mu L \cdot L^{-1}$ CO_2			500 $\mu L \cdot L^{-1}$ CO_2			700 $\mu L \cdot L^{-1}$ CO_2		
	$\bar{X}$	SD	C_V%	$\bar{X}$	SD	C_V%	$\bar{X}$	SD	C_V%
6：00	2.01	0.61	7.96	2.98	0.18	6.04	4.99	0.06	1.20
8：00	5.27	0.25	4.37	6.75	0.48	7.11	9.35	0.12	1.28
10：00	4.35	0.39	8.97	5.69	0.08	1.41	11.01	0.26	2.36
14：00	2.71	0.03	1.11	3.93	0.63	16.03	6.98	0.07	1.02
16：00	2.38	0.11	1.49	2.47	0.18	7.29	3.92	0.09	2.30
18：00	-0.83	0.29	34.9	-0.75	0.16	21.33	-0.51	0.13	25.49

Note : $\bar{X}$ –mean, SD—Standard deviation; C_V%–percentage in change

Table 2. Daily changes of temperature, relative humidity, intercellular CO_2 concentration and photosynthetic active radiation at different CO_2 concentrations

Environmental CO_2 concentration	Influential factor	Daily change					
		6: 00	8: 00	10: 00	14: 00	16: 00	18: 00
350 $\mu L \cdot L^{-1}$	Temperature(℃)	11.9	24.0	32.7	31.6	23.8	6.0
	Relative humidity(%)	46.1	40.9	31.3	38.9	40.0	54.7
	Stomatal conductance ($mol \cdot m^{-2} \cdot s^{-1}$)	381.8	323.3	171.2	134.0	345.8	92.9
	Intercellular CO_2 concentration ($\mu mol \cdot mol^{-1}$)	390.2	270.4	160.4	230.5	339.5	523.6
	Photosynthetic active radiation ($mol \cdot m^{-2} \cdot s^{-1}$)	64.9	290.1	796.2	473.7	161.6	0.9
500 $\mu L \cdot L^{-1}$	Temperature(℃)	13.9	24.5	26.5	31.3	22.6	6.9
	Relative humidity(%)	46.5	40.2	37.4	33.0	40.4	54.4
	Stomatal conductance ($mol \cdot m^{-2} \cdot s^{-1}$)	334.8	371.8	292.5	222.0	225.0	158.2
	Intercellular CO_2 concentration($\mu mol \cdot mol^{-1}$)	384.0	294.8	297.5	293.4	348.8	494.2
	Photosynthetic active radiation($mol \cdot m^{-2} \cdot s^{-1}$)	114.6	342.2	346.7	117.8	159.6	0.8
700 $\mu L \cdot L^{-1}$	Temperature(℃)	18.6	25.5	27.2	28.1	21.9	6.7
	Relative humidity(%)	42.8	44.2	38.0	35.8	39.5	60.2
	Stomatal conductance ($mol \cdot m^{-2} \cdot s^{-1}$)	287.2	286.6	401.5	308.2	259.9	274.1
	Intercellular CO_2 concentration($\mu mol \cdot mol^{-1}$)	606.1	399.9	312.8	519.6	588.1	752.0
	Photosynthetic active radiation($mol \cdot m^{-2} \cdot s^{-1}$)	169.4	449.1	771.6	432.5	140.2	1.8

Temperature

The effect of temperature on photosynthesis is very complicated. Light reaction and dark reaction are two aspects of photosynthesis. Temperature has no any effect on light reaction. Oppositely, dark reaction is a series of complex enzymatic reaction that relates to temperature. As to dark reaction, the velocity of enzymatic reaction will be enhanced with the elevation of temperature, meanwhile the velocity of changes in quality and destroy of enzyme will be accelerated. Therefore, the relation between dark reaction and temperature is the same as any enzymatic reaction that has the highest, lowest and suitable temperature. As to NPR, temperature has influence either on photosynthesis or on respiration.

Air temperature will increase with the elevation of CO_2 concentration. Effect of temperature on photosynthesis relates to species. Every species has its suitable range of temperature. Relation between NPR of *Pinus sylvestriformis* and temperature concerns respiration, because the velocity of elevation of respiration is faster than photosynthesis. Lower temperature affects the speed of dark reaction and limits NPR. Table 2 and Fig. 2 showed that with the elevation of CO_2 the NPR increased with temperature rising. At 700 $\mu L \cdot L^{-1}$ CO_2 NRP begins to lower near the temperature point of 30℃, while at 500 $\mu L \cdot L^{-1}$ and 350 $\mu L \cdot L^{-1}$ CO_2, the NPRs begin to decrease at 27℃ and 24℃. Therefore, elevated CO_2 promote the upper limitation of photosynthetic suitable temperature. From Fig. 2, we can see obviously that the higher the concentration of CO_2 is, the more rapid NPR descend from its highest point of temperature.

Relative humidity

Fig. 3, we can see that the highest NPR occurred at different points of relative humidity. The highest value of NPR matched higher relative humidity under the condition of elevated CO_2. This indicated that elevated CO_2 could weaken the negative influence of the excessive high relative humidity on NPR. Plant absorbs water passively and mineral materials by root what depends on transpiration can reduce the temperature of leaves. So transpiration has a huge influence on photosynthesis of plant. Effects of relative humidity on photosynthesis realize by affecting transpiration of plant. High relative humidity can restrain transpiration so that photosynthesis is restrained. From Fig. 3B and Fig. 3C, we can see that elevated CO_2 reduced this effect of higher relative humidity on photosynthesis. The value of relative humidity that restrains photosynthesis is the highest under 700 $\mu L \cdot L^{-1}$ CO_2, followed by under 500 $\mu L \cdot L^{-1}$ and that under the condition of 350 $\mu L \cdot L^{-1}$ CO_2 is lowest.

Stomatal conductance

Stoma is make up of a pair of defensive cells that move concern many factors, such as light, water, CO_2 concentration and temperature. It is the passage of water transpiration and CO_2 absorption. NPR under 500 $\mu L \cdot L^{-1}$ CO_2 increased with the raise of stomatal conductance (Fig. 4 B and C). The trend of NPR which changed with the alteration of stomatal conductance under 700 $\mu L \cdot L^{-1}$ CO_2 is the same as that under the 500 $\mu L \cdot L^{-1}$ CO_2. However, NPR begins to decline when the stomatal conductance reach 400

mmol·m^{-2}·s^{-1} at 700 μL·L^{-1} CO_2. The reason is that the concentration of CO_2 reaches saturation point.

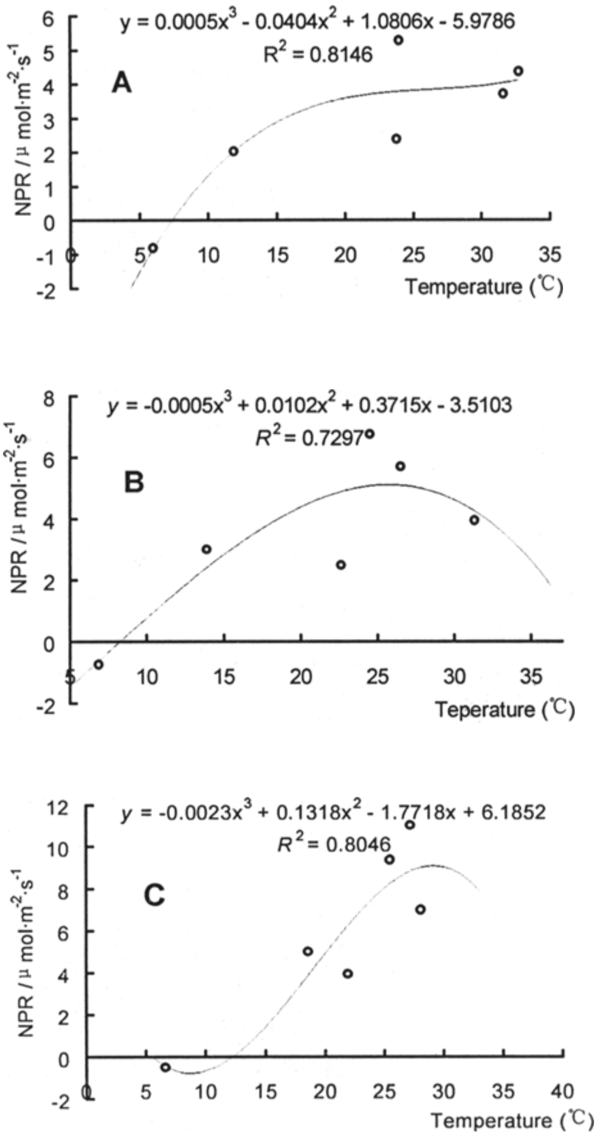

Fig. 2. Relation between NPR of *Pinus sylvestriformis* and temperature at different CO_2 concentrations
A—350 μL·L^{-1}; B--500μL·L^{-1}; C--700μL·L^{-1}

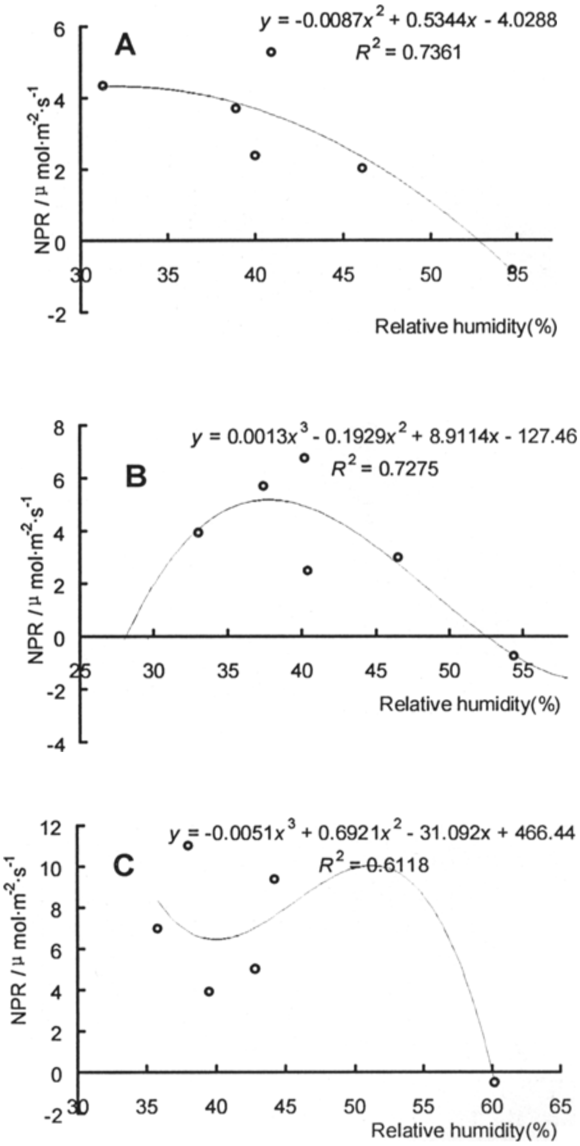

Fig. 3. Relation between NPR of *Pinus sylvestriformis* and relative humidity at different CO_2 concentration
A—350 μL·L^{-1}; B--500μL·L^{-1}; C--700μL·L^{-1}

At 350 μL·L^{-1} CO_2, the relation between NPR and stomatal conductance is different from the situation under the condition of the two elevated CO_2. NPR goes up with the elevation of stomatal conductance before its value near 240 mol·m^{-2}·s^{-1}, and from this value of stomatal conductance the NPR begins to decline and reach zero near the point of 400 mol·m^{-2}·s^{-1}. This indicated that CO_2 is a limit factor to photosynthesis of *Pinus sylvestriformis* under ambient CO_2 concentration.

Intercellular CO_2 concentration

From Fig. 5 A-C, it is evident that NPR has a decline trend with elevation of environmental CO_2 concentration. At the same intercellular CO_2 concentration NPR has highest value at 700 μL·L^{-1} CO_2 and has lowest value at 350 μL·L^{-1} CO_2. The concentration of intercellular CO_2 has a descend tendency with the elevation of environmental CO_2 concentration. This phenomena could be explained by the theory of

traditional plant physiology.

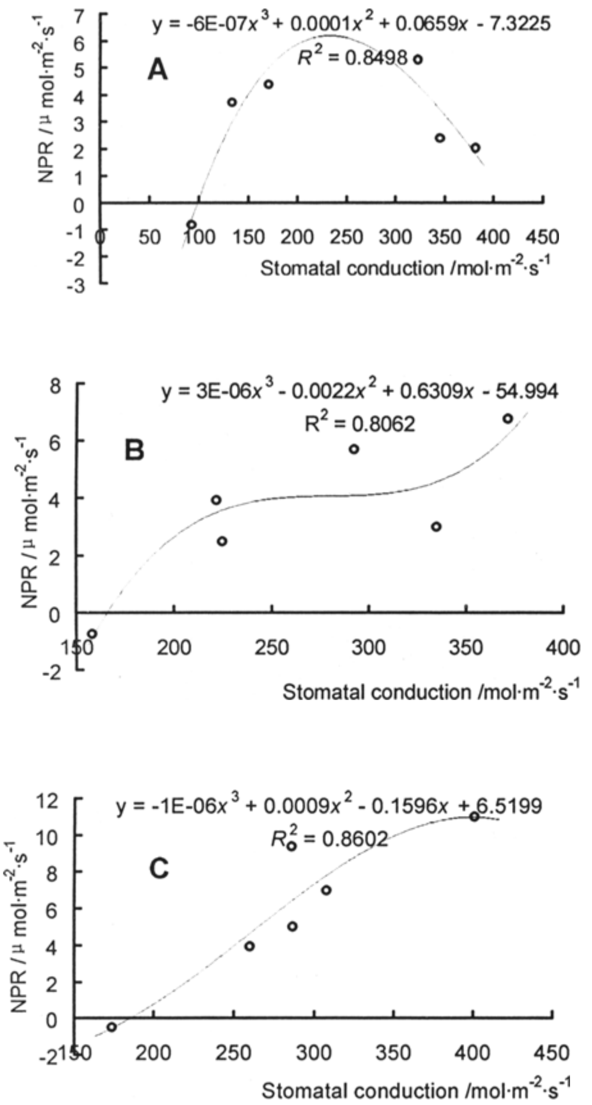

Fig. 4. Relationship between NPR of *Pinus sylvestriformis* and stomatal conduction at different CO_2 concentrations
A—350 $\mu L \cdot L^{-1}$; B--500$\mu L \cdot L^{-1}$; C--700$\mu L \cdot L^{-1}$

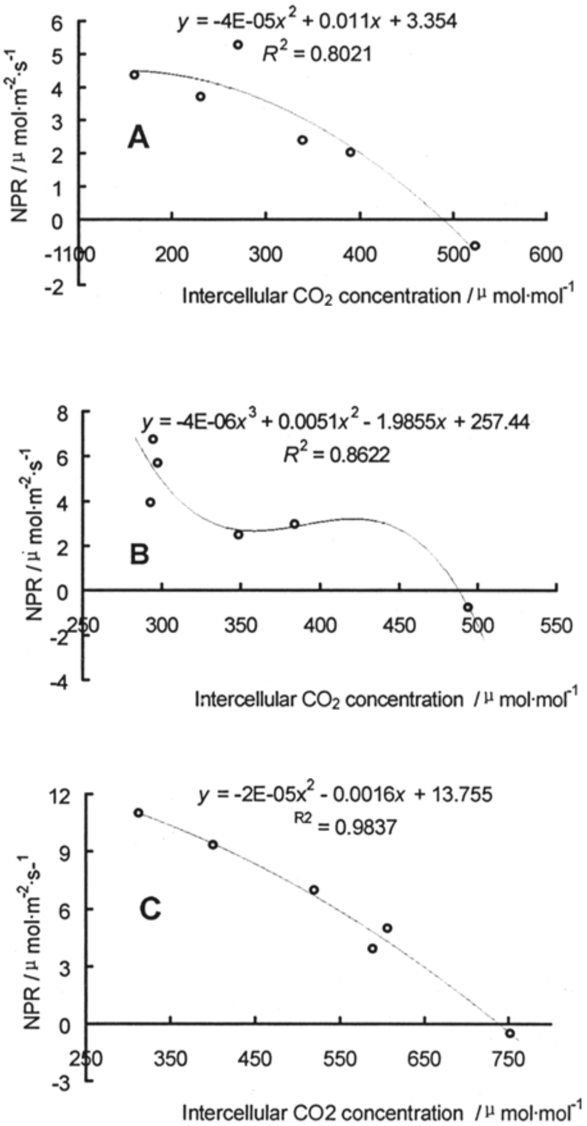

Fig. 5. Relationship between NPR of *Pinus sylvestriformis* and intercellular CO_2 concentration at different CO_2 concentrations
A—350 $\mu L \cdot L^{-1}$; B--500$\mu L \cdot L^{-1}$; C--700$\mu L \cdot L^{-1}$

True photosynthesis is the quantity of assimilating CO_2 under light, therefore, it is an important aspect of deciding photosynthesis that CO_2 enter the organ of plant. Stoma is the main passage for leaves absorbing CO_2. The spread rate of CO_2 from atmosphere to leaf decided by the difference of CO_2 and the resistance of spread. This conception can be expressed $F = \Delta C' / R'$, where F is the rate of CO_2 spread; $\Delta C'$ is the difference of CO_2; R' is the resistance of spread.

The drive strength of CO_2 spread is the difference of CO_2 concentration between atmospheric CO_2 concentration and CO_2 concentration of position where photosynthesis advances. Therefore, The quantity of CO_2 enters inside of plant will be restrained with the elevation of intercellular CO_2 concentration, and the highest NPR occurred on the point of higher intercellular CO_2 concentration at different level of CO_2 concentration.

PAR

Three regression curves of the relation between NPR of *Pinus sylvestriformis* show great resemblance (Fig. 6 A-C). Under 350 $\mu L \cdot L^{-1}$ CO_2 the NPR increase with the elevation of PAR, and the trend begins to weaken when PAR is near 500 $mol \cdot m^{-2} \cdot s^{-1}$. This result may be caused by lower temperature in

autumn. It is clear that elevated CO_2 break the low temperature limitation. *Pinus sylvestriformis* has higher NPR under elevated CO_2 than NPR under ambient CO_2 concentration. Furthermore, NPR under 700 $\mu L \cdot L^{-1}$ CO_2 is higher than NPR under 500 $\mu L \cdot L^{-1}$. CO_2.

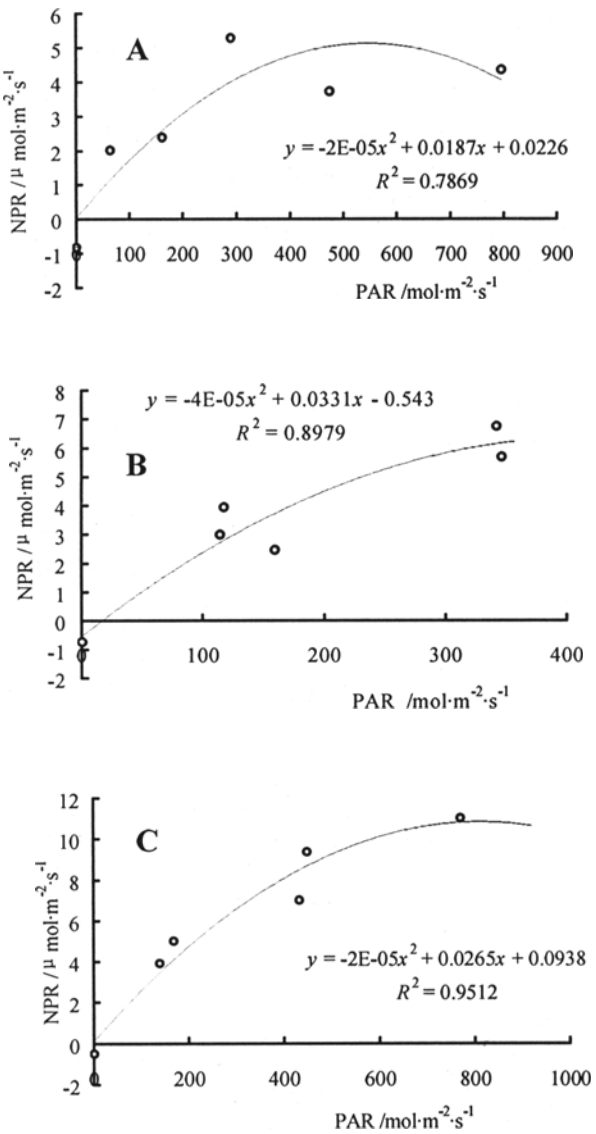

Fig.6. Relationship between NPR of *Pinus sylvestriformis* and PAR at different CO2 concentrations
A—350 $\mu L \cdot L^{-1}$ B--500$\mu L \cdot L^{-1}$ C--700$\mu L \cdot L^{-1}$

Discussion

Plant biologists have known some of the effects of high CO_2 levels on plants, and greenhouse growers have used CO_2 fertilization to increase plant yield. Work on plants from natural ecosystems has lagged behind that on crops, but in the last few years, has produced a large body of information. The major emphases have been on individual physiological traits, but the consequences of these responses for the whole plant, population, and ecosystem are less understood and, in some cases, counter-intuitive. Many plant and ecosystem attributes will be directly or indirectly influenced by elevated CO_2. Therefore, after briefly addressing physiological responses at the leaf level, we ought to concentrate our work on growth, allocations, and some ecosystem level attributes (Bazzaz 1990).

Study on photosynthetic response and its influential factor analysis of *Pinus sylvestriformis* to elevated CO_2 is elementary and tentative in this paper. In order to forecast changes of forest ecosystem in CO_2 elevated world accurately, further research involves various tree species at different scale urgent need to do in this field.

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